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Representing the Object of Controversy: The Case of the Molecular Clock

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ABSTRACT – Through a case study of the controversies surrounding the molecular clock, this paper examines the role of visual representation in the dynamics of scientific controversies. Representations of the molecular clock themselves became objects of controversy and so were not a means for closure. Instead visual representations of the molecular clock became tools for the further articulation of an ongoing controversy.

KEYWORDS – Molecular Clock, Controversy, Representation, Kimura, Ayala.

In the early 1960s Emile Zuckerkandl and Linus Pauling began comparing the newly generated amino acid sequences of proteins. When they compared sequences of hemoglobins from different species, they discovered that the differences were "approximately proportional in number to evolutionary time" (Zuckerkandl and Pauling 1965, 148). In other words, the rate of amino acid substitution was approximately constant. In 1965, Zuckerkandl and Pauling christened this constancy the molecular clock (Zuckerkandl and Pauling 1965; Morgan 1998).

Since its introduction, the molecular clock has been heralded by some as "the most significant result of research in molecular evolution" and reviled by others as utter nonsense (Wilson *et al.* 1987; Simpson 1964). The disputes that swirl around the molecular clock have questioned its variability, its timescale, its applicability, its supposed mechanisms, and its very reality (Zuckerkandl 1987; Dietrich 1998). As an object of scientific inquiry, the molecular clock seems inescapably mired in controversy.

As a timekeeping device, the molecular clock was inherently stochastic. The "ticks" of the clock were not uniform, but were best understood as a regular statistical process producing a distribution of rates of substitution for the molecule under consideration. Some variability in the molecular clock was thus expected. Nevertheless, since its inception, scientists have been concerned about how variable the molecular clock can be and still be considered a clock.

The tension between variability and constancy in the molecular clock was captured in its dominant form of visual representation: a scatterplot diagram with a line representing the central tendency of the points graphed (see Figure 1). This linear form of representation captures the unavoidably statistical character of the clock: as a statistical object, the molecular clock is an aggregate characterized by a central tendency and dispersion from that tendency. The linear representation of the clock depicted the constancy of the clock in its line through the data points, while the variability of the clock was captured by the position of many of the data points away from the line.

In this paper, I am concerned with how the linear representation was established as a stable graphical depiction of the molecular clock yet remained open to interpretation. The linear representation of the clock, I argue, depicted not one side or another in the controversy over the variability of the clock; instead, it represented the object of controversy itself. Following Bruno Latour's analysis of visual representation as tools of persuasion, the linear representation of the clock was used to persuade but not with regard to the question of variability in the clock controversy (Latour 1990). Instead of seeing visual representations as generating controversy closure, I will propose an independent role for visual representations in the inauguration and articulation of scientific controversy.

The Molecular Clock and The Problem of Variability

When they introduced the molecular clock in the 1960s, Zuckerkandl and Pauling invoked both natural selection and random genetic drift as possible mechanisms for the clock (Morgan 1998). This interpretation changed when, in 1968, Motoo Kimura argued that many substitutions at the molecular level were not subject to natural selection. Instead these neutral changes were governed by random drift (see Dietrich 1994; Suarez and Barahona 1996). Kimura, with Jack King, Thomas Jukes, and Tomoko Ohta, made the case for neutral molecular evolution in part with an appeal to its explanatory power in the case of constant rates of molecular evolution (Kimura 1968; King and Jukes 1969; Ohta and Kimura 1971).

In the late 1960s and early 1970s, advocates of neutral molecular evolution presented it as a radical alternative to the omnipotence of natural selection in biological evolution (Kimura 1983; Jukes 1991). Jack King and Tom Jukes even dubbed neutral molecular evolution "Non-Darwinian", in a successful attempt to provoke organismal evolutionary

biologists (Dietrich 1994; 1998; Hagen 1999). Random genetic drift, at least partially, displaced selection at the molecular level because a large number of observed molecular changes were postulated to be free from natural selection or were very weakly selected; that is to say, a large number of mutations were understood to be neutral or nearly neutral (Kimura 1968; King and Jukes 1969). Although advocates of neutral molecular evolution set off a long standing controversy with selectionists, hypotheses and models of neutrality and drift fundamentally shaped the field of molecular evolution through the 1970s to today (Ohta and Gillespie 1996).

An important consequence of what Kimura called the neutral theory of molecular evolution was that the rate of substitution for neutral changes was equivalent to the rate of mutation. Substitutions were detectable changes in molecules (either proteins, RNA, or DNA). If a mutation was selected, then the process of selection could cause the rate of substitution to differ significantly from the rate of mutation. The rate of substitution for selected changes would then depend on changes in the population size and environment. In the neutral case, nothing should cause the rate of substitution to become significantly different from the rate of mutation.[1] Moreover, because the rate of mutation was understood to be the result of a stochastic process similar to radioactive decay, the rate of substitution could also be understood as a constant generated by an underlying stochastic process.

The rate of amino acid substitution was known from the beginning (1965) to vary among different proteins. The neutralists explained this difference in terms of different proteins having different fractions of neutral mutants; the number of neutral mutants depends on the functional constraints for each protein. So, for instance, fibrinopeptide A has a much higher rate of substitution than histone IV, which is highly constrained (King and Jukes 1969, 792). But even within protein families variation was observed. So, for instance, insulins in the line leading to guinea pigs seem to have evolved faster than insulins in other lines (King and Jukes 1969; Ohta and Kimura 1971, 19). The neutralists needed a way to explain these deviations from the supposed intrinsic rate of molecular evolution.

In 1971, Tomoko Ohta and Motoo Kimura analysed these variations in proteins statistically. When Ohta and Kimura did this for different alpha and beta hemoglobins and for cytochrome c, they found that observed variance in the beta hemoglobin and the cytochrome c were quite large.

[1] Now a number of factors are known to intervene between mutation and substitution (see Gillespie 1991).

From this they concluded that "the variations in evolutionary rates among highly evolved animals are larger than expected from chance" (Ohta and Kimura 1971, 21). Ohta and Kimura did not take this as a reason to give up the neutral theory. The increased variance in substitution rates was chalked up to a small fraction of advantageous mutations that effected the molecule's function but did not interfere with the constancy of the overall rate of substitution (Ohta and Kimura 1971, 23).

By as early as 1974, however, Walter Fitch and Charles Langley argued that the rate of substitution was not as uniform across different lineages as it ought to be if the neutralist explanation was correct (Langley and Fitch 1974). Similar conclusions stressing the non-uniformity of rates in hemoglobin and a slowdown of rates in primate lineages were offered by Goodman, Moore, and Matsuda (1975). In 1981, Morris Goodman used the variability in the clock to argue against the existence of the molecular clock and against Kimura's explanation of it in terms of the neutral theory (Goodman 1996). By 1983, even Kimura himself admitted that the rate of molecular evolution was not perfectly uniform (Kimura 1983, 79), but in his opinion, "emphasizing local fluctuations as evidence against the neutral theory, while neglecting to inquire why the overall rate is intrinsically so regular or constant is picayunish. It is a classic case of 'not seeing the forest for the trees'" (Kimura 1983, 85).

Kimura backs up his account of rate constancy in his 1983 book, *The Neutral Theory of Molecular Evolution*, by providing a more thorough statistical treatment of the variations in the rate of molecular evolution. Kimura's analysis uses what has since been called a star phylogeny (Gillespie 1991). The lineages in a star phylogeny are taken to have all diverged from a common ancestor in a relatively short period of time. Kimura considers the case of six mammals, humans, mice, rabbits, dogs, horses, and cattle, which diverged from each other about 80 million years ago (Kimura 1983, 76). What Kimura wants to know is "whether the intrinsic rates of amino acid substitutions among the six lineages are equal and whether variation of the observed numbers of substitutions as shown lie within the limits of normal statistical fluctuations" (Kimura 1983, 76-77). In order to see if the variation in amino acid substitutions among lineages is larger than expected, the ratio of the observed variance to the expected variance, R, is calculated. But, for Poisson processes, the mean is equivalent to the expected variance, so R can be readily computed as the ratio of the observed variance to the mean and the value of R should be 1. Of the different molecules that Kimura considered, beta hemoglobin and cytochrome c showed significantly higher variation than expected. In Kimura's words, "these results suggest that although the strict constancy may not hold, yet a rough constancy of the evolutionary

rate for each molecule among various lineages is a rule rather than an exception" (Kimura 1983, 79). Moreover, Kimura notes that the average value of R for the five molecules he considered is 2.6. This value, he claims, is consistent with earlier results showing that observed variances up to 2.5 times larger than expected are allowable, if the variation is a result of chance alone (Kimura 1983, 79; Ohta and Kimura 1971). So, in the end, Kimura admits that an approximate rate constancy holds as a rule, but he also admits that there may be deviations from the rule – hence, his admonition about not seeing the forest for the trees.

The tension between variability and constancy in the molecular clock is in part unavoidable because the clock is inherently statistical. How much variability or dispersion can be tolerated depends on how the constancy of the clock itself is interpreted. Some biologists thought of the molecular clock as an average: it referred to the average rate of substitution for a given population of molecules or molecular sequences (Langley and Fitch 1974). Other biologists, however, thought of it as more than an average. They thought of the clock as an intrinsic property of individual molecules. For them, averaging over a population of molecules each with their own individual rate was a means of discerning the underlying intrinsic rate of that type of molecule (Kimura 1983).

This subtle difference in the interpretation of the statistical constitution of the molecular clock reflected profound differences in the kinds of mechanisms proposed for the clock (selective v. neutral) as well as in the value of formulating general principles or laws for evolutionary processes. For instance, Allan Wilson extended Kimura's argument concerning "the rule of the molecular clock" and its exceptions by framing it in terms of a larger conceptual divide (Wilson, Ochman and Prager 1987). Wilson and his co-authors admit that there will be exceptions to the rule of the molecular clock but, like Kimura, they emphasize its so-called intrinsic rate. Faced with the twin phenomena of a statistical mean and variation about that mean, Wilson, Ochman, and Prager argued that one had to choose either the perspective of a Naturalist or a Biochemist. The Naturalists cherish each individual molecule and its unique historical trajectory. As a result they emphasize variability rather than the mean. Wilson believed that naturalists needed to adopt the Biochemists' perspective. In his words,

> Biochemists can agree with naturalists that every nucleotide position has a unique history, as does every atom of gas. But, they also recognize that the universal gas law (PV=nRT) was not discovered by the detailed analysis of the behavior of individual atoms. Bringing together molecular biology and natural history in the search for general laws of evolution requires, as many naturalists now recognize, a willingness to transcend "microscopic" analysis. (Wilson, Ochman and Prager 1987, 246)

From the Biochemists' perspective, the constancy of the rate of molecular evolution was the important phenomena, not the variability. Neutralists, like Kimura and Wilson, argued that different types of molecules had characteristic intrinsic rates of evolution. So, all cytochrome c molecules, for instance, shared the same intrinsic property of evolving at approximately the same rate. The rate of each molecule-type was determined by the rate of mutation and the distribution of conserved and nonconserved sites.[2] Highly conserved sites were inferred to remain unchanged because alterations would hamper the molecule's function and so be selected against. Nonconserved sites changed freely and so were considered to be free from selection. (Dietrich 2006)

Selectionist critics were undeterred by Kimura's and Wilson's arguments. With growing evidence that rate variability was much more pronounced than had been supposed, John Gillespie proposed a selectionist episodic molecular clock that he claimed could explain patterns of substitution better than Kimura's neutralist explanation (Gillespie 1984). In order to answer Gillespie's claims, neutralists revised their models of substitution to accommodate greater variability (Takahata 1987). High variability in the molecular clock for many molecules is now widely accepted. This high variability has forced neutralists to revise their explanations for rate constancy and has provided an opening for selectionist explanations that can explain both patterns of constancy and variability (Takahata 1987; Gillespie 1986, 1991). However, the amount of variability that can be accommodated by the clock concept remains an open question (Ayala 1986; 1999).

Representing Constancy and Variability

From its christening in 1965, the key feature of the molecular clock has been its purported constancy. This constancy was represented graphically as a linear relationship between time and numbers of substitutional differences. R.E. Dickerson's representation of the rates of evolution for three different molecules is an early exemplar of this Linear Representation of the clock (see Figure 1). Dickerson's diagram is a Cartesian coordinate graph with time on the x-axis and the corrected number of amino acid changes on the y-axis. The timescale used is a geological timescale which includes both dates in millions of years and the names of the different eras. The rates of evolution for fibrinopeptides,

[2] The rate of mutation was assumed to be the same for all molecules. According to Kimura, it was produced by DNA replication error. Some lineages could show divergent rates (slowdowns) if DNA repair mechanisms improved in that lineage.

hemoglobin, and cytochrome c are represented as straight lines. The slope of each depicts their rate, with fibrinopeptides being the fastest to evolve and cytochrome c the slowest. Different divergence times are also noted as evolutionary landmarks (a complement to the stratigraphic timescale of the x-axis).

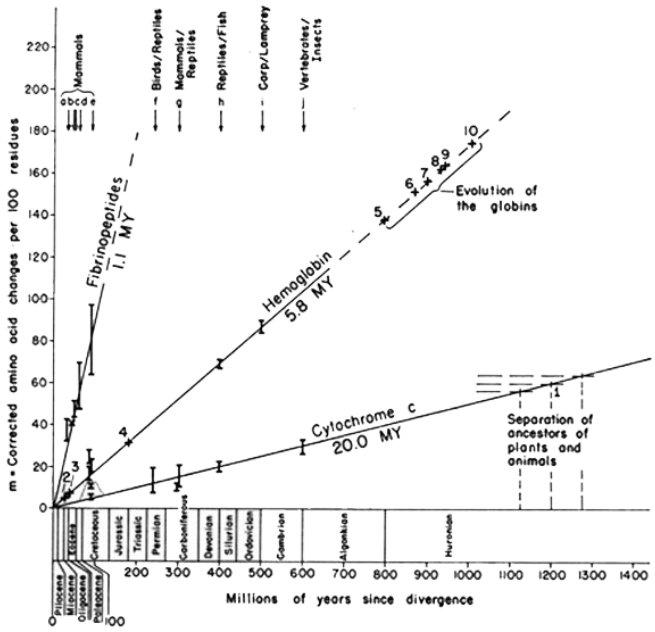

Fig. 1 - R. E. Dickerson's linear representation of the molecular clock (Dickerson 1971, 37).

The linear representation of the clock captures its statistical features by displaying the idea of constancy and variability in the same diagram. In 1974 Charles Langley and Walter Fitch produced a now widely reproduced linear representation as part of their important paper questioning the constancy of the clock (Langley and Fitch 1974). Their diagram depicts rate constancy as a straight line and its depicts each comparison as a point in the graph (see Figure 2). The line only intersects with a few of the data points. The scattering of data points off of the line depicts the variability of the clock. If the clock were perfectly constant, all of the data points would be on the line. Notably in their diagram, a cluster of points is well below the line. Next to these Langley and Fitch have inserted the word "primates". This group of points depicts what

is called the "primate slowdown" (Goodman 1996). In other words, for some reason the rate of molecular evolution seemed to slowdown in primate lineages when compared to the rate in other mammals. The "primate slowdown" was an important exception to the molecular clock and was a serious challenge for its advocates. Representationally, this cluster of points drew the viewers' attention away from the line representing constancy toward this important instance of variability.

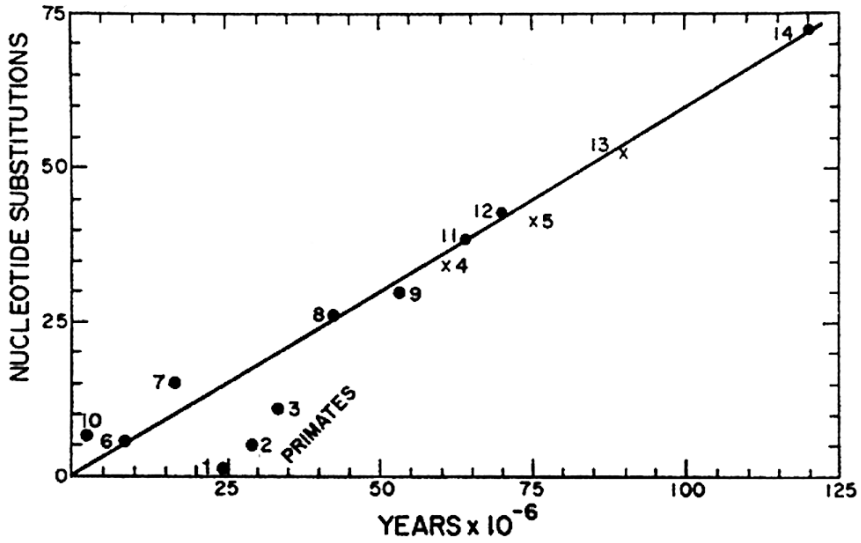

Fig. 2 - Langley and Fitch's linear representation of the molecular clock (Langley and Fitch 1974, 171).

Use of the linear representation of the clock is very widespread within molecular evolution. Both advocates and opponents of the clock used the linear representations, although different sides emphasized different features of the same visual representation. In the dispute over the extent of the clock's variability, for instance, John Gillespie and Motoo Kimura both used linear representations of the clock (Gillespie 1991; Kimura 1983). In particular, the Langley and Fitch diagram serves as the basis for a number of subsequent linear representations in review articles and textbooks (Fitch 1976; Wilson *et al.* 1977; Graur and Li 2000).

Representation and Controversy

In his classical essay on visual representation, Bruno Latour presents an image of science as a series of "agonistic encounters" between author/scientists. Latour's agonistic image of science has had its critics (Latour 1990; see also Latour 1987). I do not want to defend it as a general view of science, but I do think it is an appropriate and useful approach when considering scientific controversy. Controversies by definition are extended disputes. The dynamics of a controversy are necessarily antagonistic, although the degree of polarization and animosity certainly fluctuate over the course of a dispute.

In so far as reasoned arguments contribute to controversy closure, visual representations of data, phenomena, concepts, and models can be powerful tools of persuasion. According to Latour, scientific authors, with their twin goals of enrolling allies and defeating opponents, use inscriptions to create objects which are "mobile but also immutable, presentable, readable, and combinable with one another" (Latour 1990, 26). Consistent reproduction of an image or of certain features of an image does not guarantee the consistent reproduction of any given interpretation of that image, however. Visual representations, like experimental results, can be subject to regress unless there is some agreement on their form and meaning. Yet, if these inscriptions are to be effective instruments of persuasion in agonistic encounters, they cannot be subject to endless reinterpretation. How then is the interpretation of an inscription stabilized long enough for it to have force in a scientific debate?

Latour proposes that within a community and a specific context, a cascade of representations can train a community to see a representation and, in doing so, create consensus about the interpretation of a representation. Producing an effective representation in the context of a controversy is tantamount to winning a small battle – creating an oasis of consensus around a figure or a graph, or, in Latourian terms, black boxing a representation (Latour 1987).

In the case of the molecular clock, the linear representation of the clock is backed by a long cascade of inscriptions that render the linear form of the representation relatively immutable. The chain of inscriptions linking the linear graph of the clock to the laboratory and the field begins with a sample organism – a plant or animal from which protein or DNA is extracted. This molecule carries with it an inscribed history of its origins on its label, but it will be transformed as it is degraded, sequenced, and rendered into an string of letters from an "informational macromolecule". Individual protein or DNA sequences must then be aligned with each

other in order to make comparison of similar or corresponding regions possible. This process of alignment frequently requires that the original sequence be reinscribed as gaps are added to allow different areas of sequence to more closely correspond to each other. Because each gap is understood as a hypothetical evolutionary change, inserting gaps proceeds with caution. Pairs of aligned sequences are then redescribed numerically in terms of their similarities and differences. The number of differences in the sequences will become a marker of their evolutionary divergence.

However, what is seen in the comparison of sequences may not reveal all of the changes that a molecule has experienced. It is possible that a single amino acid or nucleotide has changed several times, yet we can only observe the most recent divergence. As a result, the number of observed differences between two sequences must be corrected. Without any access to how the molecule actually changed over time, the scientist will deploy a model of sequence evolution that will allow her to estimate the expected number of differences and then correct the observed number of differences.

The numbers generated by pair-wise comparison of molecules from different species, for instance, are next compiled into a matrix of differences. One of these differences is then made temporal by using a "known" date of divergence for the pair of organisms or species being compared. This association allows scientists to calculate the rate of evolution and associate each difference in the pair's sequences with some period of time (one nucleotide change, for instance, may indicate 10,000 years of evolution). The molecular clock concept is then invoked. Assuming that the molecular sequences have been changing at a constant rate, then each molecular difference in all of the pairs compared can be reinscribed in terms of time. As a result, the numbers of differences can then be plotted relative to time on a Cartesian coordinate graph. The scattering of points is a temporal and graphical redescription of the matrix of differences. The assumption of constancy is made visible by a line fitted to the points (often using least squares regression).[3]

In some publications, Kimura and others included diagrams of the aligned sequences and the matrix of differences (Kimura 1983). In later publications, the cascade of inscriptions behind the linear representation is not presented, perhaps because it is no longer thought necessary. In any case, the cascade of inscriptions allows the researcher to present a particular linear representation. The form of the graph, plotted data

[3] The intricacies of inferring a molecular clock are only hinted at in this somewhat general description. A more detailed description is presented in Graur and Li 2000.

points, and fitted line are accepted and stabilized as forms. Put a slightly different way, the cascade of inscriptions describes a process of inferring and representing a molecular clock that is recognized as justified within a community of scientists.

That everyone learned to recognize and understand the linear representation of the clock does not entail that this diagram was persuasive within the dispute over the constancy and variability. The cascade of inscriptions allowed scientists to manufacture an agreed upon representation, but that representation depicted both the variability and the constancy of the clock. The fitted line corresponds to a constant rate of evolution for the molecule in question, while the deviation of some of the data points from that line depict the problem of variability in that inferred rate. As a result, Kimura could use a linear representation as he argued for an intrinsic molecular clock (Kimura 1983), and Langley, Fitch, and Gillespie could use a linear representation as they argued that there was too much variability and that the constancy was in fact a statistical artifact – a mere average (Langley and Fitch 1974; Gillespie 1991). In short, the form of representation was stable, but its meaning or interpretation was not. From a Latourian perspective, the cascade of inscriptions had produced an immutable representation, but one that lacked persuasive force in the dispute at hand. In the case of the molecular clock, the linear representation was not an agonistic tool – a weapon of persuasion, but rather it represented the object of the controversy itself. As such, the linear representation was not a tool of persuasion as much as a site of persuasion: it functioned as a site of mediation where differences of interpretation could be expressed.

Mutating the Linear Representation

The power of the linear representation of the clock was recognized even by those who oppose the clock. Francisco Ayala, for instance, has been one of the most astute critics of the molecular clock, marshalling evidence of its exceptions and inconsistencies (Ayala 1986; 1997; 1999; 2000; Rodriguez-Trelles *et al.* 2001). Dreams of a universal clock that would apply across all molecules were abandoned almost immediately, if indeed they were ever taken seriously. However, the idea that every molecule had a constant intrinsic rate of change was only challenged when Ayala and others began to demonstrate that some molecules, such as superoxide dismutase (SOD), were very erratic and so not reliable as molecular clocks (Ayala 1986). This initial note of caution was amplified by Ayala as he demonstrated that variability in rates of evolution

rendered other molecules useless as clocks across genera and taxonomic families (Ayala 2000). Ayala's arguments contributed to selectionists' skepticism about the intrinsic constancy of the clock. Certainly, Ayala would have disagreed with Wilson and Kimura that biologists should ignore variability in favor of constancy.

Interestingly Ayala makes his case that some molecules are too erratic to be clock-like using linear representation diagrams. In his group's analysis of three protein molecules (GPDH, SOD, and XDH), the number of amino acid replacements for each protein is plotted relative to time (see Figure 3). Each molecule gets its own graph, but each graph has at least three lines fitted to the data: one corresponding to the comparison within *Drosophila* species (Da), one for comparison between drosophilid genera (Di), and one for comparison with other dipterans (Ce). The movement from *Drosophila* species to dipterans represents comparisons from closely related species to more distantly related insects. The expectation is that the more closely related species should be more similar and therefore have diverged more recently. The typical molecular clock assumption would be that the rate of evolution or divergence should be the same for closely related species and for distantly related insects. Indeed this ability to estimate over great periods of time is precisely what makes the clock useful for estimating phylogenetic divergence. In the study from Ayala's group, only XDH seems to have a reliable clock. This is represented by the closeness of the three lines fitted to the data. In the case of GPDH and SOD, the three lines diverge dramatically indicating that the inferred clock from comparing *Drosophila* with other dipterans is very different from the inferred clock for comparisons of closely related *Drosophila* species. Defenders of the clock are then burdened with trying to explain why the rate of evolution should vary so much for a single molecule. Such rate variability could be explained by important selected differences, but to do so would deny that the molecule had a clock and that neutral mutation could explain a constant rate of change (Rodriguez-Trelles *et al.* 2001).

In terms of representations of the clock, the strategy of the Ayala group highlights both the stability and instability in the linear representation. The stability of the clock representation is realized by its form. The data points and fitted line communicate the inferred clock. Where earlier diagrams communicated the problem of variability with widely scattered points, Ayala's diagrams reify that variability in divergent lines of constancy for the same molecule. The widely spread lines of the SOD graph (Figure 3) strongly resemble the spread lines on Dickerson's 1971 representation of the clocks in three very different molecules (Figure 1). The visual challenge is clear: if Dickerson's graph depicted three different clocks, shouldn't we infer that there are three different clocks

in SOD and GPDH? Scattered points cannot be dismissed as outliers as easily when they are rendered as justified clock inferences represented as fitted lines in the graph.

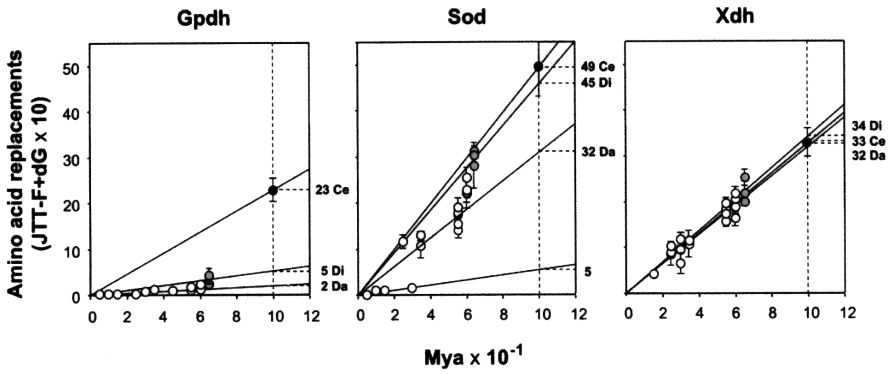

Fig. 3: Francisco Ayala's representation of molecular clocks (Rodriguez-Trelles *et al.* 2001, 11407).

Ayala's mutation of the linear representation renders it a "mutable mobile", contrary to Latour's perspective on representation. However, the persuasive force of Ayala's representation depends on the earlier form of linear representation. In effect, the earlier form of representation has become part of the cascade of inscriptions underlying Ayala's new depiction.

Conclusion

During the course of the molecular clock controversy, different aspects of molecular clocks have been visually represented in different diagrams. Specific phylogenetic hypotheses inferred with the aid of the clock have been represented in various evolutionary tree diagrams, for instance. In this paper, I have focused on the dispute over the interpretation of constancy and variability inherent in the clock as a statistical construct. The twin elements of constancy and variability were widely represented as a graph with a scattering of points and a line of best fit. Following Latour, I claimed that this linear representation of the molecular clock was stabilized within the molecular evolution community by a cascade of inscriptions. However, rather than produce an instrument of persuasion as a result, the "immutable mobile" produced is a representation of the

object of controversy rather than a partisan or persuasive representation. As such, the linear representation of the molecular clock acts as a site of mediation and communication, rather than of persuasion with regard to the question of rate variability. In this case, the linear representation as "immutable mobile" does not mark a route to controversy closure. Instead, it marks the visual articulation of a specific dispute and so helps define the terms in which that dispute is expressed.

The power of the linear representation is also embodied in its selective alteration by Ayala and his group. Using similar cascades of inscription, they produced linear representations that deviated from earlier forms. In a sense, the earlier immutable mobile is itself mutated. When considered together these related forms of representation would have to be thought of as mutable mobiles. However, where the earlier linear representation could be deployed by either side in the dispute, Ayala's multi-linear diagram is partisan – it is much more difficult to reconcile with the claim that each type of molecule has an intrinsic clock. The multi-linear diagram thus functions in the dispute much as Latour postulated that "immutable mobiles" should: it is part of a persuasive argument in an ongoing dispute. However, the contrast between the earlier linear representation and the later multi-linear representation demonstrates that not all stable, "immutable" representations produced in the context of scientific controversy are necessarily partisan. Moreover, if the multi-linear diagram furthers the molecular clock dispute by advocating a route toward closure, the linear diagram also furthers the development of the controversy by articulating the terms under dispute and opening a site for communication and mediation.

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